PROC. ENTOMOL. SOC. WASH.
105(1), 2003, pp. 108–119

SUBCORTICAL CAVITY DIMENSION AND INQUILINES OF THE LARVAL LOCUST BORER (COLEOPTERA: CERAMBYCIDAE)

KRISTIN ANN LARSON AND DAN MYERS HARMAN

Appalachian Laboratory, 301 Braddock Road, Frostburg, MD 21532, U.S.A. (e-mail: kranlars@yahoo.com; harman@al.umces.edu)

Abstract.—Subcortical, pre-tunneling cavities made by the locust borer (*Megacyllene robiniae* Forster) on the black locust (*Robinia pseudoacacia* L.) tree were studied in western Maryland on three site types: strip-mine, roadside, and old field-pasture. A number of invertebrates, associated with sap, frass, and boring dust within the cavities, were collected and identified. The more common cavity taxa included two suborders of mites, three nitidulid genera, nematodes, and two dipteran families. Mean numbers of mites were significantly greater in strip-mine sites than in roadside and old field-pasture sites. Cavity size was not related to abundance or diversity of cavity taxa, and cavity taxa did not appear to affect locust borer survival.

Key Words: *Megacyllene robiniae*, inquilines, cavities, survival, *Robinia pseudoacacia*

The locust borer (*Megacyllene robiniae* Forster) is a severe and persistent pest of the black locust (*Robinia pseudoacacia* L., Leguminosae) tree throughout its natural and extended range in North America. Its original range was thought to have been limited to the Appalachian chain from Pennsylvania to Georgia and west to the Ozark Mountain region (Cuno 1930). The locust borer is not present in Europe, however, where black locust has been planted extensively. The borer is univoltine (one generation per year), primary (invading only living trees), and host specific (invading only black locust).

Locust borers deposit eggs into the bark crevices of black locust tree trunks in later summer and fall. Tiny, newly hatched larvae penetrate the inner bark, where they overwinter. In the following spring, they resume their tunneling activities, and enlarge subcortical excavations in cambium and sapwood forming cavities of variable size. From its cavity, a larva extends its tunnel into sapwood and heartwood. The larva maintains the tunnel opening, through which it pushes excess boring dust and frass during development, and through which it emerges as an adult after pupating within its tunnel (Hopkins 1907). The host tree attempts to close a borer wound by depositing tissue around its perimeter; however, a healthy larva normally maintains and enlarges both its tunnel entrance and its cavity. Hall (1942) observed larvae restricting activities to cavity-making, without subsequent tunneling, during a drought year.

As an adult attraction to flowers is a behavioral feature of many cerambycids, locust borer adults are commonly seen congregating on blossoms of goldenrod, *Solidago* spp., particularly *S. altissima*. While on these flowers, in close association with stinging wasps and other vespids, borer adults appear to exhibit Batesian mimicry (Garman 1916, Blackwell and Powell 1981). Madden (1996) stated that when handled, borer stridulation also mimicked that of vespids. Similarly, we have noticed that when handled, borers stridulate rapidly in an apparent excitation mode, and emit an unpleasant odor, apparently in defense.

We also have verified the persistent presence of certain insect groups, particularly those in the Diptera and Coleoptera (Nitidulidae), displaying an attraction to sap and frass exudation at trunk surfaces near locust borer entrance holes. McCann (1992) identified adult insects collected from trunk surfaces on or near (within 10 cm) the entrances of active borer mines, however, his studies did not include the opening of cavities, or any inquiry into inquilines within cavities. He reported nine coleopteran species, representing five families. Little other information is available in the literature. In the present study, outer tree bark was chipped away to fully expose the cavities and analyze their contents. This procedure revealed a protected habitat with a sap and frass food source, inhabited by a guild of other invertebrate species.

Predators and parasitoids appear to have only limited effects on locust borer populations. Locust borer studies have documented predation by a garden spider (*Argiope aurantia* Lucas) on adults (Van Tyne 1983, Harman and Harman 1987, Echaves et al. 1998), woodpeckers on larvae (Hall et al. 1938, Hall 1942, McCann 1992), and ants on eggs (Echaves et al. 1998, Van Tyne 1983). In an unpublished three-week study, from late August through early September, D. Harman and J. McCann observed no instances of avian predation in a field of goldenrod, heavily used by locust borer adults. For this study, an observer sat at the edge of field with binoculars prepared to identify any birds approaching goldenrod blossoms in the field. Observations were conducted for two hours each, in morning (7–9 a.m.), midday (11–1 a.m.), and evening (6–8 p.m.) for 21 days (the last week in August through the second week in September) in 1989. During the borer larval and pupal stages, some predation by woodpeckers occurs. The predation is usually light and varies locally (McCann 1992). The same was observed for predation by garden spiders and ants.

The term inquiline has gained entry into recent biological literature, defined with slightly different slants. An ecological glossary describes the term as "... a type of symbiosis in which one or more organisms exists in the burrow, nest, or abode of another without harming the host" (Lincoln et. al 1986). The term is used for various situations including abodes of mammals, birds, and insects. Inquiline biology addresses a range of biological concepts including such items as phenological timing for nutritional resources (Shibata 2001, Eliason 2000), and the roles of predation and food limitation in species abundance (Kneitel and Miller 2000). This study addressed inquiline response to continuous wounding of living tree tissue by a woodboring larva, which created the food source.

The cavity inhabitants reported in this study are added to the list of organisms known to live close to borer larvae and may potentially affect or influence larval development. The objectives of this study were: (1) to identify inquilines in locust borer cavities, (2) compare their populations among different habitats and cavity sizes, and (3) to determine whether these inquilines affect locust borer larvae. In overview, this study addressed the subject of strip-mine reclamation and revegetation, as black locust is an important reclamation species. An extensive literature review, which narrowed the scope of the investigation, included few studies addressing biological control of the locust borer.

Materials and Methods

Sites that provided a variety of conditions were selected for sampling. Three site types differing in soil disturbance levels were in decreasing order of disturbance: strip-mine, roadside, and old field-pasture. A total of nine sites (three of each site type) were selected within a 50 km radius of Frostburg, Maryland. These habitat types were selected because they were seen as the most prominent and distinct habitats supporting growth of black locust, whose ecology is typically that of a "pioneer" species on open lands. As a minimum size requirement, each site contained an area large enough to accommodate a 15 m × 15 m study plot containing 50 or more trees of approximately 10–20 years of age. Plot corners were established and tree positions were numbered and mapped. In each plot, black locust was the predominant woody species, and stocking densities were similar.

A total of 288 samples of bark sections containing locust borer cavities were removed from each of the nine sites during the period of active larval tunneling, late May through July, 1995. Borer activity was identified by the presence of yellow sap, boring dust, or both, emanating from tunnels and visible on trunk surfaces. Four active larval cavities per site were taken weekly from randomly selected trees. Each tree had two rectangles of bark, approximately 2.5 × 5.0 cm, containing locust borer cavities removed. The bark was carefully removed using a chisel and ax handle, and then placed in a plastic bag. Bark adjacent to the selected cavities was removed, when necessary, to include all parts of larger cavities. Each cavity was placed in a petri dish and examined under a dissecting microscope within 24 hours. To locate all invertebrates, samples were broken into small sections after initial examination. Cavity invertebrates were counted, sorted, and placed in 80% ethanol for further identification.

A second major approach involved trapping. Wire cages stapled over cavities, tunnel entrances, or both were used to capture locust borer adults and associated cavity-dwelling invertebrates as they emerged later in the season. The traps were constructed by folding and stapling finely meshed copper screen into teepee-like forms of approximately 4.0 cm wide × 8.0 cm long. Traps were in place from late June through July, 1995, on trees 5–15 cm in diameter at breast height (dbh). Trap edges were caulked to prevent the escape of inhabitants. For trapping, each of the nine sites was subdivided into thirds, on each of which 15 traps were placed on randomly-selected trees, totaling 405 traps. The number of traps per tree varied from one to five, depending upon numbers of active tunnels. Whenever visible, boring dust was removed from traps and examined for the presence of invertebrates, which were counted and preserved. Entomologists from the Smithsonian Institution, the USDA Systematic Entomology Laboratory, and Frostburg State University assisted in identification of cavity and trap inhabitants. However, specialists were not available for all families and for some, the other sex, life stage, or caste was needed for further determination.

For each cavity, cavity length, width, depth, and adjacent bark thickness were measured at their greatest points, and volume was calculated from these measurements. Field observations indicated that the larvae excavated the cavities prior to tunneling, and that the cavities increased in size only slightly, if at all, after tunneling began. If a tunnel was present, the tunnel diameter was also measured. Success of borer attacks was evaluated using McCann's (1992) criteria and larval status was recorded as "died as an early instar" if little or no tunneling occurred beyond the cavity; "died after tunneling" if tunneling extended into the sapwood, but tunnel entrance diameter measured less than 4 mm; and "emerged as an adult" if tunnel entrance diameter exceeded 4 mm.

All trees within the study plots were mapped and individually numbered. Height, dbh, and resistance to pulsed electric current (an index of vigor) were measured for all trees from which cavities were removed. Three electrical resistance readings per tree were taken in mid-September over a 1-week period, and averaged. The Shigometer® (Model OZ-67, Osmose® Wood Preserving Co. of America, Inc., Buffalo, NY) provided an estimate of tree vigor by delivering a 0.5-A pulsed electric current to the cambium layer (Carter and Blanchard 1977). More healthy trees show lower electrical resistance readings than less healthy ones (Shigo 1982). Readings were taken 1 m above ground level.

To obtain a mean site age, three trees from which cavities were removed were randomly selected for each of the nine sites. Ages were obtained from increment borings. Site indices were calculated from a set of black locust curves (Kellog 1936) for each of the three site types using the heights of trees and mean site age. Site quality relates to the growth in height of most commercial tree species. For a specified age, sites of better quality produce taller trees and a higher index value (Wenger 1984).

Statistical analyses.—The Statistical Analysis System (SAS) (SAS Institute 1988) was used for all statistical analyses. Fisher's least significant difference (LSD) test was used to find possible differences among means of site type and cavity size, site type and tree measurements, and cavity size and borer survival. Cavities of insufficient dimension were excluded from statistical tests. Fisher's LSD test was also used to look for significant differences among means of site type and numbers of species. Only the four most frequent cavity taxa were included in the ANOVA. Chi-square tests were used to compare cavity size class versus borer survival, and versus site type (SAS Institute 1988). Chi-square tests were also used to compare tree vigor, indicated by the classes of electrical resistance readings, and borer survival. Linear regressions compared cavity volume against total invertebrates, and against the four more frequent cavity taxa. Pearson's correlation coefficient tested numerical relationships among the four more frequent cavity taxa.

Results

Cavity taxa.—Invertebrates collected from tree cavities represented 12 orders, 20 families, an estimated 50 genera, and about the same number of species. Invertebrate inquilines starting with the most abundant taxon were mites (Astigmata (97% of all mites) and Mesostigmata), nematodes (Rhabditida and possibly others), nitidulid larvae (primarily *Glischrochilus* spp. and *Crytptarcha* spp.), odiniid larvae—with the preceeding two larval families found in all nine sites, three collembolan families, xylomid larvae (*Solva* sp.), *Armadillidium* sp. (Isopoda), Staphylinidae, ants (Formicidae), and Miridae (Table 1).

Trap taxa.—Invertebrates collected from boring dust in traps on trunks represented 13 orders, 30 families, an estimated 53 genera, and about the same number of species. Invertebrate inquilines starting with the most abundant taxon were nitidulid larvae (primarily *Glischrochilus* spp. and *Cryptarcha* spp.), xylomid larvae (*Solva* sp.), mites (Astigmata and Mesostigmata), dermapterans (Forficulid sp.), collembolans (Poduridae), *Armadillidium* sp., chloropid spp., clerid larvae, and nematomorphs (Gordioidea) (Table 2).

Numbers of species.—Species per cavity ranged from zero to six. The four more frequent cavity taxa followed by the percentage of cavities that they were found in were mites (66%), nitidulid larvae (47%), nematodes (23%), and odiniid larvae (21%). Numbers of species, which included only the four more frequent cavity taxa, were not significantly different among site types ($P > 0.05$). Mean numbers of nematodes, nitidulid larvae, and odiniid larvae were also not significantly different among site types ($P > 0.05$). However, mean numbers of mites were greater on strip-mine sites ($F = 3.70$, df $= 2,186$, $P = 0.027$) than roadside and old field-pasture sites. Pearson's Correlation Coefficient showed a weak positive relationship between mites and odiniid larvae per cavity ($R = 0.36861$, $P = 0.0078$).

Cavity volume and taxa.—The regression of the total number of insects per cavity versus cavity volume did not show a significant linear relationship ($P > 0.05$), nor did the regressions of the numbers of indi-

Table 1. The more common invertebrate taxa extracted from subcortical cavities in black locust trees, showing numbers of individuals by site type, i.e., strip-mine, roadside, and old field-pasture. This table includes taxa occurring in numbers greater than five, represented in all three site types, or both. Other less common taxa, with their total occurrences, and specific ant spp. include Gastropoda, Stylommatophora, Haplotrematidae, *Haplotrema concavum* (Say) (1); Arachnida, Araneae, Thomisidae (2), Agelinidae (1), Salticidae, *Habrocestum pulex* (Hentz) (1); Acari, Oribatida (4), Prostigmata (1); Diplopoda (1); Insecta, Coleoptera, Cleridae, *Enoclerus* sp. (1), Histeridae, *Hololepta fossularis* Say (2), Coccinellidae (1), Trogositidae (1); Dermaptera, Forficulidae (2); Psocoptera (3); Hemiptera, Anthocoridae, *Calloidis temnostethoides* Reuter (4); Hymenoptera, Encyrtidae (1), Formicidae, *Solenopsis molesta* Say (4), *Crematogaster lineolata* (Say) (2), *Leptothorax ambiguus* Emery (1), *tetramorium caespitum* (L.) (1), *Tapinoma sessile* (Say) (1). Possible Mesostimgata include Uropodidae, Ameroseiidae, and Parasitidae. Immature Nitidulidae are primarily *Glischrochilus* and *Cryptarcha* spp., with some *Soronia* spp. *Solva pallipes* (Loew) identified as most likely sp. as it is more common than the other *Solva* sp. in eastern North America (*S. crepuscula* Hull).

Taxon	Strip-Mine	Roadside	Old Field-Pasture	Total
Nematoda				
Secernentea, Rhabditida	1,378	770	890	3,038
Arthropoda				
Malocostraca, Isopoda, *Armadillidium* sp.		16	1	17
Arachnida, Acari				
Astigmata	4,879	627	2,124	7,630
Mesostigmata	123	44	81	248
Insecta, Collembola				
Entombryidae/Isotomidae	6	16	28	50
Poduridae	7	2	8	17
Hemiptera, Miridae				
Lopidea robiniae Uhler	4	1	1	6
Coleoptera				
Staphlinidae				
Immature	2		6	8
Adult	3		3	6
Nitidulidae				
Immature	182	171	115	468
Adult	8	5	1	14
Carpophilus lugubris Murray	1			1
Erotylidae, *Megalodacne heros* (Say)	1	1	1	3
Diptera, Xylomidae				
Solva pallipes (Loew)—immature	9	4	9	22
Odiniidae—immature	30	27	52	109
Hymenoptera, Formicidae	3	6		9

viduals of the four more common cavity taxa versus cavity volume.

Cavity size and borer survival.—Borers survived to the pupal stage and presumably emerged from 50% of cavities, tunneled into sapwood and died in 13% of cavities, and died before creating a tunnel in 37% of cavities. Some size variation occurs among locust borers, in relation to sex (females larger than males) and other unknown factors, but this feature was not compared with cavity size. When comparing mean cavity measurements and survival of borers, the cavities of adult borers that emerged were significantly longer, wider, deeper, and greater in volume than those of larvae that

Table 2. The ten more common taxa from screen traps placed over borer cavity entrances and the types of sites in which they were located. Other, less common taxa and numbers of each include Gastropoda, Haplotermatidae, *Haplotream concavum* (Say) (1); Arachnida, Araneae, Agelenidae (1), *Agelenopsi* sp. (1), Clubionidae, *Clubiona pallens* (Hentz) (1), Salticidae (1); Insecta, Coleoptera, Erotylidae, *Megalodacne heros* (Say) (3), Histeridae (1), Staphylinidae (5), Trogositidae (3), Nitidulidae, adults (6); Collembola, Entombryidae/Isotomidae (3); Hemiptera, Anthocoridae *Calloides temnostethoides* Reuter (3); Homoptera, Coccidae (1), Membracidae, immature (2), Psyllidae (1); Neuroptera, Chrysopidae, *Chrysoperla rutilabris* (Burm.) (2); Diptera, Anthomyiidae (1), Ceratopogonidae, *Forcipomyia* sp. (1), Loncheidae (1), Odiniidae, immature (4), *Traginops* sp. adult (1); Drosophilidae (8), Phoridae (1), Muscidae (1), Tachinidae (1); Lepidoptera, immature (4); Hymenoptera (1); Proctotrupoidea (2), Formicidae (1), *Formica subsericea* Say (1). Immature Nitdulidae are primarily *Glischrochilus* and *Cryptarcha* spp., with some *Soronia* spp. *Solva pallipes* (Loew) identified as most likely sp. as it is more common than the other *Solva* sp. in eastern North America (*S. crepuscula* Hull). *Gaurax* sp. near *G. pseudostigma* Johnson, likely a new species. S = strip-mine, R = roadside, O = old field-pasture.

Taxon	Site Types	No. Sites	Total Individuals
Nematomorpha			
Gordioidea	S,R	2	9
Arthropoda			
Malacostroca			
Isopoda, *Armadillidium* sp.	S,R	3	16
Arachnida			
Acari, Astigmata	S,O	3	44
Mesostigmata	S	1	16
Insecta			
Collembola, Poduridae	S	2	28
Coleoptera, Nitidulidae—immature	S,R,O	9	184
Cleridae, *Enoclerus* spp.—immature	S,R,O	4	11
Dermaptera, Forficulidae			
Forficula auricularia L.	S,R,O	5	31
Diptera, Xylomidae			
Solva pallipes (Loew)—immature	S,R,O	9	82
Chloropidae	R,O	2	14
(*Fiebrigella catalpae* Mallach—11)			
(*Coniscella hinkleyi* Malloch—2)			
(*Gaurax* sp.—1)			

died shortly after entering the xylem, and those that died after entering sapwood. Mean bark thickness was not significantly different among the three groups (Table 3).

Chi-square test results revealed significant differences in survival of borers among cavity size classes ($\chi^2 = 115.526$, df = 8, $P = 0.001$). Over 95% of borers emerged from cavities ≥1,001 mm^3 (class 4 = 1,001–2,000 mm^3 and class 5 = 2,001–6,000 mm^3), while only 13% of borers emerged from cavities ≤100 mm^3 (class 1). Sixty-eight percent of borers emerged from cavities 501–1,000 mm^3 (class 3). Cavities from 101–500 mm^3 (class 2) showed little differences among the 3 borer classes (Fig. 1).

Cavity size and site type.—When comparing the means of cavity measurements by site type, cavities in strip-mine sites were significantly larger than roadside and old field-pasture sites in terms of length, width, depth, and volume. Cavities removed from old field-pasture sites were significantly greater in length than those from roadside sites; those from roadside sites

Table 3. Mean ± standard error comparison of cavity measurements by adult borer status. Means not sharing the same lower case letter within columns are significantly different ($P < 0.05$, Fisher's least significant difference test).

Borer Status	Cavity Length (mm)	Cavity Width (mm)	Cavity Depth (mm)	Cavity Volume (mm^3)	Bark Thickness (mm)
Emerged as an adult	15.4 ± 0.5a	17.0 ± 0.6a	4.4 ± 0.2a	1,193.4 ± 80.7a	10.9 ± 0.3a
Died after tunneling	12.4 ± 1.1b	8.8 ± 0.7b	2.5 ± 0.2b	285.2 ± 43.9b	10.6 ± 0.6a
Died as an early instar	11.9 ± 0.7b	9.3 ± 0.6b	1.8 ± 0.1b	226.0 ± 34.1b	10.4 ± 0.4a
ANOVA					
F	9.63	49.32	61.3	57.1	0.56
df	2, 284	2, 284	2, 270	2, 270	2, 271
P	0.0001	0.0001	0.0001	0.0001	>0.05

were significantly deeper than those from old field-pasture sites. Mean bark thickness was significantly less in old-field pasture sites than on roadside and strip-mine sites (Table 4). Chi-square tests revealed significant differences between cavity size classes and site types ($\chi^2 = 30.115$, df = 8, $P = <0.0001$). Strip-mine sites had fewer cavities in the smallest cavity class (≤100 mm^3), and more cavities in the two larger cavity classes (1,001–6,000 mm^3) compared to roadside and old field-pasture sites (Fig. 2).

Tree measurements and site type.—Mean tree heights (m) were significantly greater ($F = 31.60$, df = 2,285, $P = 0.0001$) in old field-pasture sites (7.7 ± 0.2) than on strip-mine (6.1 ± 0.1) and roadside sites (6.0 ± 0.2); whereas, mean dbh (ranging from 5.9–6.6 cm) was not significantly different among site types ($P > 0.05$). Mean tree age (yr) was significantly greater ($F = 3.41$, df = 2,243, $P = 0.035$) in old-field pasture sites (19.0 ± 0.8) than in roadside sites (16.5 ± 0.7), but not strip-mine sites (17.5 ± 1.1). Mean electrical resistance readings (kohms) on strip-mine (16.6 ± 0.9) and roadside sites (16.0 ± 0.6) were significantly lower ($F = 6.23$, df = 2,277, $P = 0.002$) than readings on old field-pasture sites (19.2 ± 0.8). In contrast, old field-pasture sites had a higher site index value (37) than strip-mine (31) and roadside sites (32). A chi-square test indicated no significant differences in survival of borers among the four classes of electrical resistance readings ($\chi^2 = 7.680$, df = 8, $P = 0.465$).

Discussion

Cavity inquilines did not appear to have a negative effect on locust borer populations. Therefore, use of the term inquiline is qualified as no direct evidence of cavity inhabitants harming the abode-building host was found. However, little is known about the habits of many of these organisms, especially larvae. Nitidulid larvae are saprophagous in general, but may feed on fungal fruiting bodies or spores, and may be predaceous. The three genera found in borer cavities, *Cryptarcha*, *Glischrochilus*, and *Soronia*, are among genera that occur most often under fermenting bark or in rancid sap (Stehr 1991).

McCann (1992) found three *Glischrochilus* species in or within 10 cm of borer cavities. The species were *G. samquinolentus* (Olivier), *G. quadrisignatus* (Hay), and *G. fasciatus* (Olivier). Since nitidulid larvae in this study were not identified to species, they may have been represented by the *Glischrochilus* spp. McCann (1992) found. *Cryptarcha* species in this study may have been represented by *C. ampla* (Erichson), also found by McCann (1992). *Cryptarcha* spp. are known to eat scolytid eggs and larvae, but are not considered to be obligate predators (Stehr 1991).

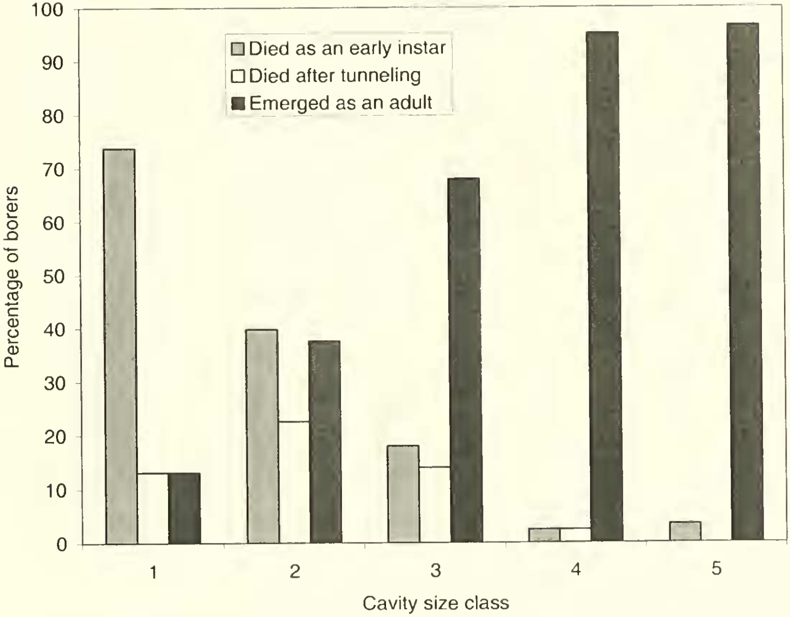

Fig. 1. Locust borer development with regard to cavity size class.

Odiniid larvae are thought to be scavengers of insect frass and other decaying organic matter. They may attack other larvae (Stehr 1991). A *Cryptarcha* larva appeared to retreat upon encountering an odiniid larva during one cavity dissection. Although odiniid larvae might be aggressive towards other cavity taxa, they seemed too small in size and low in number to have an overall negative effect on locust borers.

Xylomid larvae are thought to be scavengers on decaying organic matter or predators of insect larvae (Stehr 1991). Although xylomid larvae may be predaceous, they did not appear to have an overall negative effect on borers. Borer adults presumably emerged from cavities with xylomid larvae twice as often as they failed to emerge from cavities with them.

Mesostigmatids, commonly found in the borer cavities are mostly free-living predators. Many are external or internal parasites of invertebrates, reptiles, birds, and mammals (Krantz 1978). Because the mesostigmatids were most often found alone in the cavities, they did not appear to pose a threat to borer larvae.

Nematodes (Rhabditida and possibly other orders) were a common cavity taxon, but their affect on borer larvae remains unknown. Adult borers presumably emerged from cavities with hundreds of nematodes. Nematodes were found most often in moist cavities within surrounding tissues, and were occasionally found on dead mites and nitidulid larvae. One of the most common nematode inquilines collected from the subcortical cavities, *Myctolaimellus robiniae* n. sp. (Diplogasterida: Cylindrocorporidae), has been described (Harman et al. 2000).

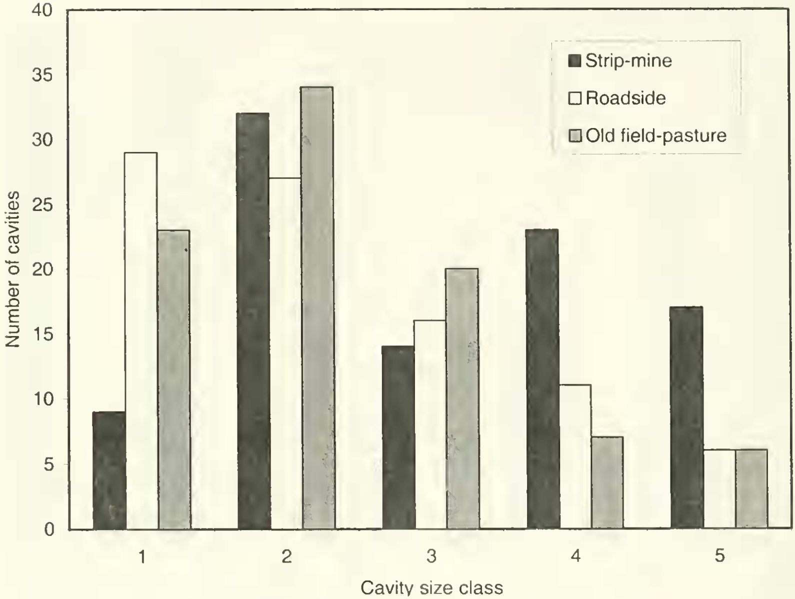

Fig. 2. Number of cavities per site type with regard to cavity size class.

and others are under investigation. The ecological role of these nematodes was not determined, but records stated that most Cylindrocorporids are saprobes, often in symbiotic relationships with insects.

Most species of rove beetles (Staphylinidae), also collected in the present study, appear to be predaceous. Conspecific staphylinid larvae and adults usually consume the same foods (Borror et al. 1989). Nineteen specimens of larvae and adults were collected from cavities and traps. Twelve checkered beetle larvae (Cleridae) were collected primarily from borer traps. Most

Table 4. Mean ± standard error comparison of locust borer cavity measurements by site type. Means not sharing the same lower case letter within columns are significantly different ($P < 0.05$, Fisher's least significant difference test).

Site Type	Cavity				
	Length (mm)	Width (mm)	Depth (mm)	Volume (mm^3)	Bark Thickness (mm)
Strip-mine	16.2 ± 0.8a	15.4 ± 0.8a	4.0 ± 0.2a	1057.4 ± 101.1a	11.4 ± 0.4a
Roadside	11.2 ± 0.6b	11.4 ± 0.8b	3.2 ± 0.2b	610.0 ± 91.8b	10.9 ± 0.4a
Old field-pasture	13.7 ± 0.6c	12.5 ± 0.7b	2.4 ± 0.2c	547.0 ± 68.6b	9.7 ± 0.3b
ANOVA					
F	13.66	7.02	15.43	10.38	5.92
df	2, 284	2, 284	2, 270	2, 270	2, 271
P	0.0001	0.001	0.0001	0.0001	0.003

checkered beetles are predaceous as larvae and adults. They are common on or within trees, where they prey on larvae of wood-boring insects, especially bark beetles (Borror et al. 1989). Both rove beetles and checkered beetles were not thought to pose any threat to locust borers, as they occurred infrequently, and were not present in the three cavity samples containing live borer larvae.

Earwigs (Dermaptera), most often found grouped together, feed primarily on dead or decaying plant matter. Some feed on living plants, and some may be predaceous (Borror et al. 1989). Like rove and checkered beetles, earwigs were thought to occur too infrequently to pose any threat to borers.

Surprisingly, Gordian worms (Nematomorpha) were found in eight traps. Nematomorphs, as juveniles, live within the body cavity of a host, usually an insect, and a host dies after its worm emerges (Pearse et al. 1987). Although Gordian worms may have been killed some borers, adult borers emerged from four traps that contained these worms.

Ants (Formicidae) were occasionally found in borer cavities. They generally appeared to be too small to pose any threat borer larvae and were probably feeding on tree sap and cavity taxa other than borer larvae. Most ant species found in cavities were considered subordinate according to Fellers' (1987) ranking of ants by dominance. Subordinate ants tend to be less aggressive and avoid other ant species.

Coleoptera and Lepidoptera appear to support the greater ranges of parasitoids (Mills 1994). Two parasitoid families (Tachinidae and Phoridae) that utilize coleopteran larvae were collected in borer traps, and one family (Encyrtidae) was collected from a borer cavity. Some Encyrtidae and Tachinidae utilize coleopteran larvae while some phorid parasitoids utilize coleopteran pupae (Mills 1994). Each parasitoid family was represented by only one specimen in this study.

Cavity size is related to advancement and survival of borer larvae, although it appears that many other determinants of cavity size are unknown. Strip-mine sites had significantly larger cavities, indicating more success among borer larvae, and yielded more mites than roadside and old field-pasture sites. A major implication regarding black locust on strip-mine sites is that stress is greater on-mine than off-mine resulting in increased vulnerability to invasion by the borer (Harman et. al. 1985), and other probable organisms. Although the locust borer is a primary invader, its success is still related to the health of its host.

The astigmatid mites found in the cavities appeared to be primarily fungivorous. Many Astigmata are saprophagous, fungivorous, or graminivorous, while some are parasitic (Krantz 1978). A colony of Astigmata from one of the cavities collected from a strip-mined site was maintained for over a year, subsisting on a diet limited to yeast pellets (K. Larson, personal observation 1996). Significantly greater numbers of fungivorous mites on strip-mine sites than off-mine may indicate greater fungal infestation, due to stress at the site.

Hopkins (1906) stated dead areas surrounding cavities, or hibernation cells, penetrate into the wood and appear to assist larvae in boring through inner bark to the wood. He also stated if the surrounding area is healthy, the larvae may not advance their tunnels into the wood (Hopkins 1906). Fungal infestation in less vigorous trees may contribute to the success of borer larvae in creating larger cavities. Wounds made by borer larvae provide an opening for fungi to enter locust trees. Damage by a heart rot fungus *Fomes rimosus* (Berkeley) Cooke a parasite of black locust, causes heartwood to become lightweight and crumbly (Hoffard and Anderson 1982). While borer larvae over-winter, fungal activity around their hibernation cells may weaken surrounding tissue to such an extent that larvae may be able to consume more tissue when they resume activity in spring, thereby increasing cavity size and improving chances of survival.

Selection of varieties of black locust resistant to fungi may reduce damage incurred by borers requiring the presence of fungi for greater survival. Unfortunately, past references to fungi in relation to locust borer ecology have been largely observational. Although mycological aspects were also beyond the scope of this study, the results indicate a need for further studies of the tree-insect-fungal relationship.

Acknowledgments

We thank Gary Hevel (Collembola, Psocoptera, Membracidae, Staphylinidae, Nitidulidae, Drosophilidae, Phoridae, Anthomyiidae, Muscidae, Tachinidae, Trogositidae, Coccinellidae, and Gelechiidae), and O. S. Flint (Chrysopidae), Smithsonian Institution; D. R. Smith (Formicidae and Encyrtidae), Natalia J. Vandenberg (larval Cleridae, Nitidulidae, and Staphylinidae), Peter Touhey (Proctotrupoidea and Lonchaeidae), A. L. Norrbom (Odiniidae), N. E. Woodley (Xylomidae), the late Curtis W. Sabrosky (Chloropidae), Thomas J. Henry (Anthocoridae and Miridae), D. R. Miller (Coccidae and Psyllidae), and David A. Nickle (Forficulidae), Systematic Entomology Laboratory (SEL), Agricultural Research Service, USDA; William L. Grogan (Ceratopogonidae), SEL cooperating scientist, Salisbury University, MD; and Wayne A. Yoder (Araneae, Acari, and Haplotrematidae), Frostburg State University, for assistance with identifications. Partial funding for the study was provided by the Maryland Agricultural Experiment Station.

This manuscript is Science Series Contribution No. 3569 of the University of Maryland, Center of Environmental Studies.

Literature Cited

Blackwell, W. H. and M. J. Powell. 1981. Observations on late season pollination of *Solidago canadensis* L. (Asteraceae) in Southwest Ohio. Castanea 2: 136–139.

Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. An Introduction to the Study of Insects, 6th ed. Saunders College Publishing, Fort Worth, Texas, 875 pp.

Carter, J. K. and R. O. Blanchard. 1977. Electrical resistance related to phloem width in red maple. Canadian Journal of Forest Research 8: 90–93.

Cuno, J. B. 1930. Utilization of black locust. United States Department of Agriculture Circular 131.

Echaves, V., D. M. Harman, and A. L. Harman. 1998. Site quality in relation to damage by locust borer *Megacyllene robiniae* Forster in black locust. Journal of Entomological Science 33(1): 106–112.

Eliason, E. A. and D. A. Potter. 2000. Biology of *Callirhytis cornigera* (Hymenoptera: Cynipidae) and the arthropod community inhabiting its galls. Environmental Entomology 29(3): 551–559.

Fellers, J. H. 1987. Interference and exploitation in a guild of woodland ants. Ecology 68: 1466–1478.

Garman, H. 1916. The locust borer (*Cyllene robiniae*) and other enemies of the black locust. Bulletin of the Kentucky Agricultural Experimental Station 29: 99–135.

Hall, R. C. 1942. Control of the locust borer. United States Department of Agriculture Circular 626, 19 pp.

Hall, R. C., W. L. Baker, H. C. Secrest, and H. A. Waters. 1938. Report on investigation of the locust borer problem conducted at the Columbus, Ohio Laboratory of the Bureau of Entomology and Plant Quarantine, 1931–1937 inclusive.

Harman, D. M. and A. L. Harman. 1987. Distribution pattern of adult locust borers, (Coleoptera: Cerambycidae) on nearby goldenrod, *Solidago* spp. (Asteraceae) at a forest-field edge. Proceedings of the Entomological Society of Washington 89: 706–710.

Harman, D. M., M. A. Van Tyne, and W. A. Thompson. 1985. Comparison of locust borer *Megacyllene robiniae* Forster (Coleoptera: Cerambycidae) attacks on coal strip-mined lands and lands not mined. Annuals of the Entomological Society of America 78: 50–53.

Harman, A. L., J. L. Winter, and D. M. Harman. 2000. *Myctolaimellus robiniae* n. sp. (Diplogasterida: Cylindrocorporidae) from larval cavities of the locust borer, *Megacyllene robiniae* Forster. Journal of Nematology 32(4): 389–395.

Hoffard, W. H. and R. L. Anderson. 1982. A guide to common insects, diseases, and other problems of black locust. United States Department of Agriculture, Forest Service, Southeastern Area, Forest Pest Management. Forestry Report SA-FR 19.

Hopkins, A. D. 1906. Some insects injurious to forests. The locust borer. United States Bureau of Entomology Bulletin 58: 1–16.

———. 1907. The locust borer and methods for its control. United States Bureau of Entomology Circular 83, 8 pp.

Kellog, L. F. 1936. Site index curves for plantations of black locust, central states region. Central States Experimental Station, no. 36.

Knietel, J. M. and T. E. Miller. 2002. Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. Ecology 83(3): 680–688.

Krantz, G. W. 1978. A Manual of Acarology, 2nd ed. Oregon State University Book Stores, Inc., Corvallis. 509 pp.

Lincoln, R. J., G. A. Boxshall, and P. F. Clark. 1986. A Dictionary of Ecology, Evolution, and Systematics. Cambridge University Press. 298 pp.

Madden, R. C. 1996. Cerambycid beetle on goldenrod. Website: http://www.marymt.edu/~madden/ceram.html.

McCann, J. M. 1992. Studies in locust borer (*Megacyllene robiniae* Forster) ecology: I. Intrastand variation in locust borer attack rate. II. Rate and characteristics of woodpecker predation on locust borers, M.S. Thesis, Frostburg State University, Frostburg, Maryland.

Mills, N. J. 1994. Parasitoid guilds: defining the structure of the parasitoid communities of endopterygote insect hosts. Environmental Entomology 23: 1066–1083.

Pearse, V., J. Pearse, M. Buchsbaum, and R. Buchsbaum. 1987. Living Invertebrates. The Boxwood Press, Pacific Grove, California. 848 pp.

SAS Institute. 1988. SAS/STAT user's guide, release 6.03 ed., SAS Institute Inc. Cary, North Carolina, 1,028 pp.

Shibata, E. 2001. Synchronization of shoot elongation in the bamboo *Phyllostachys heterocycla* (Monocotyledoneae: Gramineae) and emergency of the gall maker *Aiolomorphus rhopaloides* (Hymenoptera: Eurytomidae) and its inquiline *Diomorus aiolomorphi* (Hymenoptera: Torymidae). Environmental Entomology 30(6): 1098–1102.

Shigo, A. L. 1982. Tree health. Journal of Arboriculture 8: 311–316.

Stehr, F. W. 1991. Immature Insects, Vol. 2. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Van Tyne, M. A. 1983. A comparison of the incidence and severity of the locust borer, *Megacyllene robiniae*, on reclaimed strip-mined areas vs. non-strip-mined areas in western Maryland, M.S. Thesis, Frostburg State University, Frostburg, Maryland.

Wenger, K. F. [ed]. 1984. Forestry Handbook, 2nd ed. John Wiley and Sons, New York, 1,335 pp.